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Thesis

THE MIGRATION OF INSECTS

(With Special Reference To Butterflies)

by

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The writer acknowledges the unfailing help and encouragement which Dr. Plath has consistently given. While the contradictions and inconsistencies discovered in much of the material dealing with the subject, have made the study extremely fascinating, they have, on the other hand, made it one of unusual difficulty. Whenever trained scientific judgement has been needed, Dr. Plath has given his time and advice unstintingly.

INTRODUCTION

The purpose of this thesis has been to gather together the available information concerning insect migration, and to incorporate it into a semi-popular treatment of the subject. By "semi-popular" is meant a generalization of the subject, excluding to a great extent actual technical details of individual flights, lists, tables, charts, and the like. Mr. C. B. Williams in his book "The Migration of Butterflies" (1930) gives an extensive bibliography, which was used as a start for the investigation. The material found in this bibliography led to new material, particularly more recent writings by the same authors. The writer has attempted to sift the evidence available, and to draw what seem to be the most logical conclusions, at least until further evidence is gathered.

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CHAPTER I

THE PROBLEM

While until recently, relatively little detailed and organized information has been assembled on the subject of insect migration, nevertheless, the phenomenon appears to have been noted and commented upon since earliest historical times.

Joel, in the bible, mentions a migration of locusts through North Africa in 3800 B.C. Saint Augustine and Pliny both give evidence of insect migrations. Mouffet says, "Wert thou as strong as Milo or Hercules, and wert fenced or guarded about with an host of giants for force or valour, remember that such an army was put to the worst by an army of butterflies, flying in troop in the air in the year 1104, and they hid the light of the sun like a cloud."(1)

The natives in Ceylon account for the April and November flights of Pierids by the belief that they are flying to the top of Adam's Peak to do homage to Buddha.(2) And in Africa the southward migration of Libythea labdaca is so regular in appearance that the natives believe it to be an infallible sign that the rains have set in, and the negro peasant knows that he may safely plant his cereal crops, at any rate his maize. Toward the end of the rains, swarms of the same butter-

(1) Tutt, J.W., Migration and Dispersal of Insects: Lepidoptera. The Entomologist's Record, 1899. Vol. 11, Page 319.
(2) Tutt, J.W., Migration and Dispersal of Insects: Lepidoptera. The Entomologist's Record, 1900. Vol. 13, Page 98.

flies return northward and, from this, the native concludes that the rains are about over.(1)

In Central India, the natives declare that rain will always begin in June, three days after the coming of the butterflies. This is by no means invariably the case, but the probable explanation is that the butterflies which are going to migrate, are brought out of the pupal stage by the monsoon, although Euploea core, the butterfly involved in these migrations, is not under ordinary conditions a migratory insect.(2)

The study of insect migrations inevitably presents several definite and distinct difficulties. The first of these problems is that, until a few years ago, the available information was, in the strictest sense of the word, almost entirely non-scientific. This information consisted chiefly of notes sent to various entomological, scientific, or purely secular magazines, on flights which had been observed on various parts of the globe. And the descriptions of these flights were more likely to be a reflection of the emotions of the authors, than exact scientific data essential to make a record of real value.

The writer has in mind one article that describes a night which the author spent watching a migrating swarm of Anosia plexippus in Kansas. At the conclusion of the reading, one's impressions of the observer's emotional reactions, at having

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(1) Farquharson, C.O., The Migration of Libythea labdaca westward at Moor Plantation. Trans. Ent. Soc. London, 1921 Pages 404-405.

(2) Aitken, E.H., The Migration of Butterflies. Journal Bombay Nat. Hist. Soc., 1897. Vol. 11 Pages 336-337.

had the supreme privilege of spending a night of surpassing lovliness, viewing "such myriad swarms" of "those scintillatingly beautiful creatures" was much more vivid than his information concerning the true nature of the flight. Undoubtedly, however, the author had much of value to add to the scientific knowledge of the flight of the milkweed butterfly in the central portion of the United States, had she but understood how to properly record it. Of late years, much more exact and reliable records are being kept, possibly partly due to the oft repeated plea of Mr. C. B. Williams, that any flight observed by persons of scientific background should be recorded, and that certain definite data which he prescribed should, if possible, always be obtained.

A second difficulty is that the nature of migrations of various insects in different countries is so diversified, and the periods of migration so irregular, that few records giving information for any one species over a period of years, are yet available. For example, flight routes have not been accurately and definitely established, so that observers along these routes may be on the constant look-out for information concerning migrations. Regions where various species of migrating insects originate are not yet clearly defined. Furthermore, the goal of the migrating swarms, is in many cases still largely a matter of conjecture. In short, the present information is so limited in some directions, and so contradictory in others, that few, if any, definite conclusions may be estab-

lished. And those conclusions which seem more or less substantially established for one species, prove to be absolutely erroneous for another.

This lack of scientific certainty, however, acts as a powerful stimulus to the investigator, and the result is a keen and careful investigation of each newly discovered bit of contributory material. While, therefore, any conclusions reached are still partially hypothetical, nevertheless the evidence available is such that some worthwhile premises may be laid down as a basis for future study.

CHAPTER II

MEANING AND SCOPE OF MIGRATION

Before we can satisfactorily and intelligently commence the investigation of the migration of insects, we must establish very clearly the meaning and scope of the term migration. The word has been very commonly used in relation to the movements of birds and fish, and less commonly to the movements of certain species of mammals.

The migration of birds has been thoroughly investigated, and the migratory movement of all types of birds is well known. In the case of birds the term may apply to movements between rather widely separated areas, or to movements covering a comparatively short distance. Migration of birds, for several reasons, is much more easy to study and understand than that of insects. In the first place, the life of the average bird is of much greater duration than the life of any of the so-called migratory insects, so that each individual bird may conceivably make the migratory journey several times. Each individual of a given species ordinarily takes part in what might be called a mass movement to a new territory. Thus at one season of the year one finds the species present in abundance in a certain part of the country, while at another season that particular species is entirely lacking. This makes the time at the beginning and end of the migration clearly defined, and easy to

establish, and since migration appears in that species year after year, at approximately the same date, the gathering of accurate scientific data is by no means difficult. On the other hand, in the case of most migratory insects, not all members of a species migrate, and the dates of migration are not periodically recurrent. The life of a butterfly is of such extremely brief duration, that in no case is there any evidence of the same individual making the trip more than once, except Danais archippus, which may make the return trip. In many cases there is clearly established evidence that the same individual does not even complete one journey, but stops to breed and dies, while later on, the offspring of that generation continue the trip.

In the case of birds, certain definite causes have been assigned for the migratory instinct becoming active. The more important of these causes are, first, the absence of the specific food supply; and, second, the breeding instinct becoming active, and demanding a migration to the breeding areas. The causes of migration of butterflies are by no means as clearly understood and defined.

The size of the individual bird has made it possible to establish the practice of banding, which has enabled accurate information to be secured concerning definite individuals. For example, a young bird was banded in New Brunswick in July, 1930, and the same band was removed from the leg of an adult bird in Florida, 1934. Thus is established irrefutable evidence that

the migratory range of that species is from New Brunswick to Florida, that the breeding area is at least as far north as New Brunswick, and that the time for the northern migratory journey is prior to July. No such practice of banding, or anything comparable, could ever be established in the case of insects.

While less information is available in the case of fishes, due to the nature of their habitat, nevertheless banding of fishes is common, and we know that in many species there is a migratory journey definitely associated with breeding. In some cases the adult life of the fish is spent in fresh water, with a return to salt water for breeding; while in other cases the process is reversed, the adult life of the fish being spent in salt water with a return to fresh water ponds and streams for spawning. In any case the cause and routes are more or less well established.

Much less is known of the migratory movements of mammals than of either birds or fish. While migratory movements of the reindeer are more nearly comparable to those of birds than to those of butterflies, the migration of the lemming seems to be more like that of butterflies. It appears to result from the overcrowding of certain areas, and this results in the migration of a large group to a new environment. Differing from birds in the cause of the migration, lemming migration also differs from that of birds, in that a few members of the species are left in the old area, so that a portion of the

group continues living in the old environment, while the remainder migrates to the new one. In the case of the lemming there is no evidence of a return migration, which, therefore, is more comparable to that of butterflies.

With this necessarily brief summary of migration in the various types of animals, we may now attempt to formulate a definition applicable to migration in the case of birds and fishes. Individual students differ on some points regarding migration, but in general the consensus is, that migration is a purposeful, concerted and definitely recurring movement from one locality to another. In the case of mammals the definition must be restricted to the statement that migration is merely a purposeful movement from one location to another, with no definite recurrence.

But when we come to the consideration of the migration of insects, we find different investigators assigning all shades of meaning to the term. A few reputable scientists have declared that the nature of the insect excludes all thought of migration; that when insects are found far from their natural habitat, the air currents are entirely responsible for the flight, and that there is nothing purposeful whatever in the change of locality.(1)

The late Walter Heape in his work on animal migration distinguishes between migration and emigration. In emigration

(1) Muller, Albert, On the Dispersal of Non-Migratory Insects by Atmospheric Agencies. Trans. Ent. Soc. London, 1871. Pages 175-186.

there is no return flight, while in migration there is always a return flight.(1)

Sharpe (1892) says that the term migration should not be used except for recurrent changes in habitat; definite in direction, periodic in time, induced by instinct, and originating in the idea of some consequent benefit to the race.(2) Considering the information available today, if this were accepted as a definition, one could not accurately regard insect movements as in any sense a migration.

On the other hand, however, we find men who use the term in a much broader sense, otherwise they could not include insects as a migratory group. Poulton (1921) says that, "It is a dormant instinct, existing in all species of insects liable to outrun the food supply." And continuing, he declares that its stimulus is a want of the food plant. He also asserts that butterflies which are not normally migrant may become so.(3)

Tutt, as early as 1898, pointed out that insects are particularly well adapted to migration, because they have the power to fly immense distances; that they can go without food in the imago state for a very long period; that their bodies are extremely light; and that heat and cold do not kill migratory

(1) O'Eyrne, H., A Migratory Flight of Catopsilia eubule (Lepid: Pieridae.) Psyche, 1933. Vol. XL No. 4, Page 135.

(2) Sharpe, W.E., The Occasional Phenomenal Abundance of Certain Forms of Insect Life. Proc. and Trans. Liverpool Biol. Soc. 1892. Vol 7, Pages 17-43.

(3) Poulton, E.B., Notes on the Migration of Lepidoptera with a Suggestion as to the Cause of the Backward and Forward Flight Occasionally Observed. Trans. Ent. Soc. London, 1921. Page xiii.

insects, but rather it is their progeny which suffer.(1) And another investigator, writing about that period, advanced the opinion that migration in insects is analagous to that of birds, since its object is to find food.

Buckstone (1926) contends that a butterfly is migrating when it flies in a steady manner, keeping a bee line, with its usual distinctive flight features modified.(2)

Possibly Williams has formulated as good a working definition as any one because it is applicable to birds, fish and mammals, as well as to insects. His definition is as follows: "Migration is a periodic, more or less unidirectional, continued movement, assisted by the efforts of the animal in a direction over which it exerts a control which results in the animal passing away from its previous daily field of operations." (3)

Before attempting to discover the causes leading to the migration of the various species of insects, it may be advisable to discuss briefly the circumstances which led scientists to the conclusion that certain groups of insects do unquestionably show migratory characteristics.

First, ever since the middle of the last century, reports have been coming in from all parts of the world concerning flights seen in progress. These reports have not been sent in

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(1) Tutt, J.W., The Migration and Dispersal of Insects: General Considerations. Entomologist's Record. 1898. Page 209.
(2) Buckstone, A.W.W., Migration of Insects. The Entomologist, 1926. Vol. 59, Pages 7-8.
(3) Williams, C.B., The Migration of Insects. 1930. London, Oliver and Boyd, Pages 9-10.

by scientists alone, but also by laymen from widely separated geographical points. Butterflies in migration have their flight features so completely modified, that it would be practically impossible for any person of normal powers of observation not to notice that a distinctive and out of the ordinary journey was in progress. While reports may be non-scientific and much greatly desired information may be lacking, nevertheless each individual record of an observed flight forms a link in the growing chain of evidence that migrations do occur.

Second, the geographical distribution of the various species of butterflies is now more or less definitely known. Hence, when large groups of butterflies appear in entirely isolated regions, and especially regions entirely foreign to their habitat, it is necessarily noted and commented upon. The presence of "cotton moths" at lightships in the northern United States and Canada, when these moths cannot usually survive weather north of the cotton belt, offers exceedingly strong substantiation for the migration theory.

Third, when butterflies that are common inhabitants of one locality suddenly almost completely disappear, it is to be assumed that either they must have progressed to another stage of development, that death must have taken them, or that migration has occurred. If the disappearance takes place at a time when it is unlikely for them to undergo transformation, or if they are not yet sexually mature, and hence not ready to die, it may then be assumed that migration is the most logical explanation.

Inasmuch as in the average case not all individuals of the species migrate, this absence of a species from an area would not be complete, and therefore would be far less likely to attract the attention of the ordinary lay observer than in the two previously mentioned cases.

Fourth, almost innumerable reports from all parts of the world bring evidence that butterflies and other insects are frequently seen at sea hundreds of miles from land; are observed on the tops of high mountains, and even on glaciers; in short in places that in no sense of the word could be termed their normal habitat. White (1871) mentions fifty specimens of insects found in the snow on top of Benmucdhu, which he says were involuntarily carried there. Captain de Long, sailing in the ship Jeannette on the northeast passage through Behring Straits to the North Cape, records that he saw a butterfly seven hundred miles north of the Arctic Circle.(1) How can their presence in these out of the way places be explained, except that these individuals are migrating to a different locality?

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(1) Williams, C.B., Further Collected Records Referring to Insect Migration. Trans. Roy. Ent. Soc. London, 1933. Vol. 81, Page 114.

CHAPTER III

WHY MIGRATION CANNOT BE THE PASSIVE RESULT OF EXTERNAL FORCES

Before proceeding to the discussion of the various causes assigned for the migratory instinct suddenly becoming active, notice may well be taken of the theory frequently advanced that migration is not purposeful, but merely a passive result of external forces. The definition adopted for migration, excludes of course the idea that migration is not purposeful, but inasmuch as this theory has been and still is held by some scientists, it should not be discarded without at least a brief consideration.

The two chief agents of passive migration are ships and air currents. Anosia plexippus, which is a native of America has been found of late years in Great Britain. Some account for this phenomenon by declaring that the butterfly was brought to Europe on some of the ships crossing the Atlantic. Crews of transatlantic vessels say that when the ships leave Norfolk, Virginia, in the autumn, the butterflies are always flying about the potato lockers, and so some get inside and are thence carried to England, feeding on the potatoes as they go. When the ships land, they leave and become inhabitants of Great Britain. This butterfly is found very rarely on the West Coast of Ireland, where exponents of the carried-by-vessel theory say it would most normally be found, if it had made a voluntary flight

from this country.(1) This particular butterfly is endemic only in Central America and the southern part of the United States, hence the only source must have been on this continent, and while Frowhawk says he believes immigration to Great Britain is effected entirely by ships, nevertheless he admits that the arrival there might have been the result of a voluntary migration. The insect first appeared in Great Britain in 1876, in France in 1877 and reached Portugal and Spain in 1886. It is interesting to note that this species of butterfly has also spread westward as far as the Malay Archipelago and Sumatra.(2)

The Monarch butterfly was not well known in Hawaii until 1850, and strangely its arrival was practically simultaneous with the establishment of its food supply there. The exponent of the passive dispersal theory would say that the butterfly had been carried there with its food plant, though its habits would appear to make its being carried in its earlier stages highly improbable.(3)

Those who believe that migration is entirely due to natural causes, assign air currents as a second agent of transportation. They argue that currents of heated air carry insects along with them, with no voluntary effort on the part of the insect. On the tops of the higher mountains collectors have found insects not normally native there, which they conclude

(1) Frowhawk, F.W., On the Appearance of Anosia plexippus in Britain. The Entomologist, 1921. Vol 54, Pages 145-146.
(2) Frowhawk, F.W., The Black Veined Brown: Anosia plexippus. The Field, 1915. (April 17) Vol. 125, No. 3251.
(3) Felt, E.P., Dispersal of Butterflies and Other Insects. Nature, 1925. Vol. 116, Page 366.

have been dropped by air currents. On Mount Washington scientists have found species common in the southern United States, and the view is held that these have been carried there by currents of warm, and hence rising air, which in turn drops them as the air cooled. Whymper in his treatise on the equatorial Andes, quotes Humboldt and Bonpland to show that insects may be blown by winds to a height of 16,000 to 19,000 feet.(1) Mellows in 1924 reports that living specimens of Vanessa urticae were found 2,000 feet above the Glacier de Trient; Vanessa cardui and Macroglossa stellatarum within a few feet of one of the highest mountain peaks of the Andes, while Pieris rapae and Pieris brassicae were found 10,000 to 11,000 feet above sea level.

It is unquestionably true that air currents may well aid in the migration of insects, but in view of all evidence at hand it seems unlikely that they are the primary cause, and therefore insects are by no means merely passive passengers in the air currents. There are of course upper air currents that may be reached by the aid of convection currents 1000 feet above the surface, and the velocity of these upper air currents may be thirty, fifty, or even one hundred miles an hour. There are records of grasshoppers having been seen 2,000 feet above the surface, mosquitoes 3,000 feet, and honey bees 200 feet.(2)

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(1) Guppy, H.B., Dispersal of Butterflies and Other Insects. Nature, 1925. Vol. 116, Page 543.
(2) Felt, E.P., Dispersal of Butterflies and Other Insects. Nature, 1925. Vol. 116, Page 367.

When fuller scientific observation and study of life in the upper air currents has been made, which the aeroplane now makes possible, we may have more accurate information as to what part these currents play in the migration of insects.

In Sunda Straits, Mount Krakatoa erupted in 1883 and completely laid waste the adjacent territory. No form of life could possibly have survived its dreadful blast. Twenty years later, however, sixty-four species of insects were found there. Of course one may accept the theory that they were transported by ships and air currents, but there is abundant evidence that insects constantly make half the 2,000 mile trip to the Hawaiian Islands, in the region of the Indian Ocean. Two of the larger and stronger flying members of the dragonflies were not seen in Hawaii until comparatively recently. They are natives of this continent and are widely distributed here. Dragonflies are strong fliers and have been seen in the Indian Ocean 900 miles from Australia and 300 miles from Cocos Keeling Island, where they could not possibly maintain themselves. The evidence does not point to their having been carried passively. The almost unanimous conclusion is that while meteorology may, and probably does, play some part in insect drift, it nevertheless does not and cannot account for it.

CHAPTER IV

THE CAUSES OF MIGRATION

Admitting then, that a more adequate cause must be found for insect migration, than the explanation offered by the proponents of passive dispersal, let us turn to some of the other explanations concerning the cause of insect drift. It is assumed of course, that the instinct to migrate is latent in all migratory forms, therefore we are considering not the origin of the instinct itself, but rather the cause of that latent instinct becoming active. Some scientists even go a step farther and assert that the instinct may also be latent in forms which are commonly non-migratory, and that when some motivating influence or force arises, the instinct becomes active and the non-migratory form becomes migratory.

A recent article gives interesting information in regard to this particular point. The writers were thoroughly acquainted with the common butterfly species of New England, especially those of New Hampshire and Connecticut. Their observations included no record of the orange sulphur butterfly, having been seen among the native species in these localities prior to August, 1931. However their own observations and those of local entomologists give abundant evidence that the species is now present and becoming constantly more abundant. Apparently the insect has developed migratory tendencies, and

is invading a new territory. Whether the authors believed that this butterfly had become a permanent resident of these areas, or whether they considered this merely as an annual migration, without the establishment of a permanent home, was not made clear. Possibly it had not been definitely determined.(1)

Assuming, then, that the migratory instinct must be awakened before migration can take place, we may properly consider some of the commonly assigned causes for the awakening. The first and most fundamental of these is the matter of food shortage. And by food shortage is meant, of course, shortage of the larval food plant. This cause would satisfactorily account for the observed irregularity in the migration of various species. A certain year is often referred to as a "Painted Lady Year", by which is meant a year when there is an abnormal migration of the Painted Lady (Vanessa cardui). But no one can predict when there will be such a year. Since food shortage cannot be predicted, the migration of the butterfly cannot be predicted either.

On the other hand, Burnett describing the migration of the Cotton Worm of the United States says, "It comes always in migration like a foreign enemy, always selecting thrifty plantations." He further notes the singular fact that the migration appears at intervals of every three years. It usually appears on the seaboard first, and then moves inland. Its most exten-

(1) Britton and Harte. The Recent North-Eastward Spread of the Orange Sulphur Butterfly, Colias eurytheme Boisdv. Lepidoptera) Bull. Brooklyn Ent. Soc. 1933. Vol 28, No. 3, Pages 109-115.

sive and deadly ravages are at intervals of twenty-one years, or every seventh time of its appearance; for example, 1804, 1825, 1846, etc. No one can tell where these movements of the cotton worm originate, because the migrations are invariably made at night. It appears reasonably evident, however, that the cause of their migrations is a search for food, since they always devastate the plantations in their path. Yet why are these periodic migrations made at intervals of three years, with especially severe attacks every twenty-first year? Surely the shortage of food does not appear periodically in such a regular manner.(1)

The theory of a shortage in the food supply as cause for migration of certain species, must be interpreted more as a regular migration to areas where the supply is abundant, than a migration due to abnormal shortage. Fletcher notes that Polymmatus boeticus L. is a regular migrant every year about the middle of March. When the peas, which are the larval food supply dry up, the butterflies move northward. He also says Pieris brassicae comes in April to lay its eggs on the cabbages, and when the cabbages dry up they move on.(2)

Curiously contradictory statements are made by English observers, concerning this butterfly search for food. Some declare that as soon as the migrating hordes of butterflies ar-

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(1) Burnett, W.I., The Cotton Worm Moth of the United States. Proc. Bost. Nat. Hist. Soc., 1854. Vol. 4, Page 316.
(2) Fletcher, T.B., Notes on Butterfly Migration, Bird Attacks on Butterflies, etc. Proc. Ent. Soc. London, 1930. Vol. IV, Part III, Page 103.

rive on the English coast, they go immediately to the localities where the food supply is abundant. On the other hand, other observers declare that the butterflies show no interest whatsoever in the finding of a food supply, but upon arrival scatter more or less aimlessly in all directions.

Several causes for the absence of the food plant may be noted. The most common are, of course, purely external ones, such as floods, or drought.

Another cause which may be assigned directly for migration, and connected, though perhaps less directly with the lact of the food supply, is over-population. The Good years of reproduction, which in the case of Pyrameis antiopa have been called Painted Lady years, result in excessively large numbers of this species, or over-production. This naturally would lead to the food supply becoming inadequate, and would tend to migration.

Andrews (1922) in discussing insect drift, says he had always accepted the idea that the chief reason for migration was the insurance of an ample food supply for the next generation; and that the depletion of the food supply, followed an abnormal increase in population. The insufficiency of food due to drought is, in his judgement, a sufficient and satisfactory explanation of migration. He asserts it is conceivable that in past times the food plant existed in a belt which became sterile because of climatic and geologic changes, and so, small migrations have lengthened out.(1)

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(1) Andrews, H.L., The Migrations of Butterflies. Jour. East Africa and Uganda Nat. Hist. Soc. 1922. Vol. 17, Page 73.

Having already mentioned a "good year" several times, it may be pertinent to note that there is much difference of opinion as to what really produces a good year. Some are of the opinion that a good year for any given species follows a hard winter, because a hard winter is best for hibernating insects, since first, it decreases attacking bugs, and second, it decreases mold.(1) Others assert that a mild, dry winter is sure to be followed by a full emergence.(2) A third opinion declares that a mild winter, with a more than average rainfall, followed by a cold spring with east wind favors over-production.(3) Two more opinions may be mentioned, which are in complete divergence. The one that a moist, hot season produces over-population; the other that a drought best produces a good year. Adkin offers an explanation which is in no way dependent on meteorological conditions, but assigns the cause to a diminution of parasites and hence an increase in the species.(4)

While we have discussed at some length food shortage, search for the larval food supply, and over-population, as causes for the migratory instinct becoming liberated, various other causes have been mentioned incidentally. One of these is the sex impulse, which is doubtless decidedly unimportant,

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(1) Barrett, C.G., The Influence of Meteorological Conditions on Insect Life. Entom. Month. Mag. 1882. Vol. 19, Pages 6-7.
(2) Essig, E.O., A Butterfly Migration. Pan-Pac. Ent., 1926. Vol. 2, No. 4, Pages 211-212.
(3) Carrington, J., On the Abnormal Appearance of Colias edusa and other diurnal Lepidoptera in 1877. Entom. 1877. Vol. 10, Page 187.
(4) Adkin, R., The Abundance of White Butterflies in 1917. Entom. 1918. Vol. 51, Page 38.

since most insects are not sexually mature before they start the migratory flight. O'Byrne in describing a migratory flight of Catopsilia eubule, writes that prior to the flight large numbers of male pierids were to be seen around puddles, and this was evidence that there was over population. Such assemblages were supposedly made up of the weaker members of the species, who couldn't get food and hence began to wander. Thus, large migratory groups were being formed, and these were almost entirely composed of males. This would represent the natural elimination of the males.(1) I have, however, found no other evidence or support for this opinion.

Viewing dispassionately the large mass of contradictory opinions on the causes of the migratory instinct becoming active in butterflies, it is evident that we are yet without sufficient exact data on which to base scientific conclusions. Hunger, over production, the sex impulse, rhythm, etc. may be assigned as causes, but as yet none is indubitably established. Possibly the man who says "each migrant butterfly starts when it becomes a butterfly" and hesitates to go more deeply into the matter is, for the moment, the wisest. Furthermore, whatever is assigned as the primary force, operating to arouse the dormant instinct for migration, cannot account for the driving force that motivates migration.

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(1) O'Byrne, H., A Migratory Flight of Catopsilia eubule. Pschye, 1933. Vol XL, No. 4, Pages 131-136.

CHAPTER V

THE MIGRATION OF LOCUSTS

At this point it is pertinent to consider briefly the "Theory of the Periodicity and Migrations of Locusts", as advanced by Uvarov. While in general this paper discusses chiefly migration of the Lepidoptera, moths and other closely related forms; nevertheless Uvarov's explanation of migration, although only applicable to one species of locusts, is too valuable and too interesting to omit.

Uvarov introduces his consideration of the subject, by stating that sixteen species have been described by various authors as belonging to Locusta L. He, however, reduces the number to two, namely migratoria L. and paradalina Walk. And as the latter, in its important characteristics, differs so radically from migratoria, he creates for it a new genus, naming it Locustana g.n. Locusta migratoria L. and its several forms supply some exceedingly interesting data for the student of insect migrations.

Two varieties of Locusta are migratoria and danica. These two differ considerably in certain morphological characteristics. This has led many students to regard them as two entirely different species. However, when many specimens are examined, some individuals are always found that cannot be certainly identified as either danica or migratoria, but which seem to be

intermediate forms. This fact has led many authors to regard danica and migratoria as variants of the same species.

Studying their morphological characteristics, Uvarov noted and listed many and marked differences, which it is not necessary to record here. According to Uvarov, Dr. N. Adelung of the Petrograd Zoological Museum decided that the male genitalia of the two species differed. But when Uvarov, at Adelung's request, re-investigated this matter, he concluded that the differences were not of sufficient importance to form a basis for regarding them as of different species. The genitalia consist of several small and very complicated pieces, and while sometimes in different individuals, they do differ slightly, nevertheless these differences not being connected with the external surfaces, scarcely warrant the separation into different species.

Uvarov also concludes that while the external coloring of the two adult forms are variable, there is likewise here, not enough variation between the two forms to justify separating them into two species. However, there is a very definite color difference in the nymphal stage. The coloration of the nymphs of danica varies greatly in different individuals, while that of the nymphs of migratoria is more or less constant for all members at corresponding stages of their development.

More interesting still are the apparent differences between the two forms, when a study is made of their biology. Danica appears to have no preference for any particular type of breeding grounds. Migratoria on the other hand, is known to confine its breeding to the basins of particular rivers, and to

the deltas of such rivers as empty into them. All of these localities have more or less the same type of vegetation, consisting of a kind of reed grass, growing in such dense masses as to form a jungle sometimes with an area of hundreds of square miles. The nymphs are hatched among these reeds and later take to the reeds of the surrounding water. The climatic conditions in these various localities are almost identical; an abundance of near-tropical heat, with great humidity caused by the excessive evaporation. The insects are not always equally numerous in the several breeding grounds. In certain years, only a few isolated individuals will be noted; but year after year the swarms increase in number until a maximum is reached.

A short time after the nymphs are hatched, they collect in small groups and within a limited range, move about from place to place, attaching other groups of nymphs to them. In this way large swarms of nymphs are formed and their movements become more irregular. Some observers explain these movements as a search for food. This, however, is improbable as the insects do not eat when moving, and they continue to move no matter how abundant the vegetation.

Two other explanations are suggested for their movements. The first is heat. It is well known that the swarms do not move at night. But with the coming of the rays of the morning sun the movement of the nymphs begins, and it continues until early evening, when it slackens, ceasing altogether with the coming of darkness. On cold sunless days, there is no traveling whatsoever. The second explanation of this movement is

that each nymph has a tendency to repeat the movement of its fellows. As a result of this tendency whenever a few begin motion, all those nearby take up the movement and thus large swarms of nymphs are formed.

With the last moult of the season, however, this movement naturally ceases. Then scattered adult individuals begin to make short flights. The same tropism then takes place with the adults as occurred with the nymphs. Small groups of flying individuals merge with each other thus forming larger bands and swarms, which eventually move away and thus emigration takes place. The usual explanation of this emigration is again search for food. But this explanation cannot be accepted, for frequently the locusts leave enormous quantities of food behind them, migrating to other areas where there is little or no food to be found. A second reason may be given for rejecting this explanation. When the locusts start migration, they have large fat bodies, which during the migration grow smaller. Apparently then, during migration, the locusts live to a great extent on stored food and therefore since they apparently take little or no nourishment during the flight, food, or lack of it, has nothing to do with the cause of migration.

Rossikov, according to Uvarov, explains migrations by asserting that the migrating individuals become heavily parisitized and migrate in an attempt to rid themselves of the parasites by flight. This is improbable, however, since those which migrate are often free from parasites while those left behind are frequently heavily parisitized. Other students offer the

explanation that the locusts in migration are seeking another breeding ground. This also is improbable since apparently migration ceases when certain physiological developments are reached, and this may occur in a locality which is not at all suitable as a breeding ground.

About the biology of danica comparatively little is known. There is agreement, however, that the adults never gather in large swarms. And furthermore they rarely migrate.

Studying the invasion of locusts in 1912, Uvarov concluded that the migrating hosts consisted entirely of migratoria, and that danica was not present at all. Nevertheless when the spots where oviposition took place were located, and the emerging progeny were studied the following spring, it was clearly evident that while the vast majority of specimens were migratoria, some were undoubtedly danica, and others were intermediate forms. Uvarov reports that breeding experiments have been carried on by Plotnikov, and these have proven that danica can be bred from migratoria.

The third variety of Locusta is migratorioides. In its morphological features it is much like migratoria, and, compared with migratoria, has no new features except a modification of migratoria toward danica. It seems in all respects to be intermediate between migratoria and danica. And while conclusive evidence is lacking, it seems probable that there can be a transformation of migratorioides into danica.

It may be interesting to note here the geographical distribution of the three forms. Danica is known throughout the

whole of the eastern hemisphere except in the coldest regions, on high mountains and in waterless deserts. The distribution of migratorioides, though not quite so extensive as that occupied by danica, is practically the same save for the Palaearctic Regions. Some authorities contend that the Palaearctic Region is frequently the home of migratoria, as occasional specimens have been found even beyond it.

The three varieties of locusts thus described are, according to Uvarov, in reality only phases of the same species. There seems to be no doubt that migratorioides is the mature form of the species. The permanent breeding grounds of this variety have never been investigated. It is believed, however, that these breeding areas are in a tropical climate, and may be in jungles of impenetrable vegetation. Probably the breeding of migratorioides does not progress at the same rate but when large swarms are formed they finally migrate. When compelled by physiological causes to do so, they settle down and oviposite. Thus the second variety or danica is formed. This variety is adaptable, spreading over the territory where it happens to be. When danica reaches a breeding ground comparable to that used by migratorioides it undergoes atavism, reverting again to that phase. In this way the distribution of the species progresses through the gradual spread of danica and the migrations of migratorioides. It is well known that migratorioides are found in tropical regions, while migratoria spreads even into the Palaearctic Region. Here the swarming stage of migratorioides is represented by migratoria. When the breeding

of danica takes place in an area dissimilar to the breeding ground of migratorioides, the reverse transformation of danica into the swarming phase migratorioides does not take place, but ends with the half way phase migratoria.

Uvarov concludes his discussion as follows: "The periodicity of the locust invasions is caused entirely by the wonderful phenomenon of the transformation of the swarming locust into a solitary, harmless grasshopper."(1)

(1) Uvarov, B.P., A Revision of the Genus Locusta L. With a New Theory as to the Periodicity and Migrations of Locusts. Bull. of Entom. Research, 1921. Vol. 12, Pages 135-163.

CHAPTER VI

DISCUSSION OF MIGRANTS AND MIGRATORY FLIGHTS IN GENERAL

In sifting the large amount of material dealing with types of migrations, beginnings of the flights, behavior of the migrants, wind direction in relation to the flight, etc., the present writer found most divergent opinions. Some statements hold true for all types of migrating insects, while many others hold true for only one species, and sometimes seem applicable to but a single flight. The diversity of the evidence, however, suggests many interesting questions and, doubtless, when more complete and accurate scientific data are available, phases of the subject now obsure, will be satisfactorily explained. Included in this section, will be many data more or less uncorrelated, concerning migrants and their flights. This material may seem out of place here, but it appears to have no logical relation to any other chapter. Although much direct evidence gathered from many sources will be quoted, yet some of the conclusions drawn, will be based on the findings of William's work (1930). For he not only presents the largest accumulation of material, but apparently possesses unusual ability to draw definite and logical conclusions from the mass of often seemingly contradictory evidence.

First one may inquire how the huge migrating swarms assemble for the flight. Do all assemble in one place prior to the migration? And does the entire swarm start at one time? Or do

but a few individuals begin the flight with increasingly larger groups uniting with them, so that as the migration proceeds the swarm grows?

Prall (1898) in discussing a flight of Euploea core, suggests that first, either the swarm was so huge that it must have originated in a large area, or second, that it did not originate in one place, but assembled after hatching, or third, that it must have assembled in answer to some call.(1)

Saverner (1908) writes that he never saw Anosia plexippus flying in flocks except when the flock was disturbed, while resting in a tree. He points out that individuals very rarely passed a resting flock, without stopping and joining it, thus giving the impression that the flocks had no common origin, were not static in size, but rather had begun the flight in small numbers being gradually increased by the accession of stragglers.(2)

A most serious handicap to the study of the migrations of butterflies is the fact that with many species no one has actually observed the origin of the migrations, and there is no reliable record of how or where the migration begins. Possibly the reason so little is known about the start of the flight, is that so few species have a swarming period prior to the flight. Undoubtedly most species start their migration with only a few scattered individuals in the swarms.

Danais archippus is one of the outstanding exceptions.

(1) Prall, S. E., The Migration of Butterflies. Journal of the Bombay Nat. Hist. Soc. 1898, Vol. 11, Page 533.
(2) Saverner, P.A., Migrating Butterflies. Entomological News (1908) Vol. 19, Page 218.

There are many reliable records of the swarming of this species prior to migration. A report comes from Manitoba that about the twentieth of August in 1907 great numbers of Danais archippus gathered and stayed about ten days in one place, moving about locally during the day.(1)

Saunders (1871) furnishes a very vivid picture, of the preparation of butterflies for migration. He reports an estimate of about nine millions of butterflies gathered in trees. When they were disturbed, they would fly up and then settle back again. At times they were seen gyrating around in a wild manner. Finally they gathered and flew away.(2) Apparently, whether the butterflies start out in swarms, or separately, they possess a consciousness of power, because there are numerous records of these insects beginning their flight against a strong wind.

Many varying descriptions of actual flights while in progress are on record. Sometimes the insects travel so far apart that unless the characteristics of the migratory flight were very different from those usually marking the flight of that species, the ordinary observer would fail to realize that a flight was in progress. On the other hand, accounts of flights are recorded when the insects were so abundant that the claim is made that had windows been open, the insects would have en-

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(1) Bradshaw, George H., A Swarm of Butterflies. Ottawa Nat. 1907 Vol. 20, No. 11, Page 212.
(2) Saunders, W., On the Swarming of Danais Archippus. Canad. Entom. 1871. Vol. 3, Pages 156-157.

tered in such numbers as to almost eclipse the light.[1] From Heligoland have come frequent reports of "storms of moths and butterflies" in flight. Cramer describes a migration of the Painted Lady in 1926 through Palo Alto in the Santa Clara Valley. He reports there were thousands visible moving about fifteen miles an hour, and that motorists found their windshields and radiators clogged with them.[2]

Williams (1930), in summarizing the various kinds of flights, suggests the following different types, although there is no strong differentiation between them.

"(I) A very thin flight where the butterflies are well out of sight of each other. This type is less frequently reported because only a person who understands migration and is looking for it, would observe this kind of flight.

(II) A thin migration of individuals, where if the observer has a good outlook, he will always have three or four individuals in his line of vision. Most naturalists will recognize this and record this type of flight.

(III) This lasttype may grow more concentrated till it gets so thick that it may 'hold up motor cars', 'cast a shadow on the ground', 'cause turkeys to gobble in consternation', or 'necessitate natives walking with their heads bent to the storm.'

These three types have no sharply defined borders. (I) may merge with (II),and (III), on its borders undoubtedly merges to

(1) Thwaites, C.W., Extraordinary Abundance of Pyrameis cardui and Plusia gamma in Saxon, Switzerland. Entomologist 1879, Vol. 12, Pages 270-271.

(2) Cramer, Frank. Butterfly Migration. Nature 1926. Vol. 118, Pages 191-192.

(II). There are three other types of migration that can be recognized.

(IV) 'a compact mass sharply limited on both sides and in front and behind, much like a small swarm of locusts'.

(V) A narrow ribbon or belt which may be only a few yards wide, but which may take several hours to pass.

(VI) There may be in some migrations a wide front with the butterflies grouped in small focal points along this wide front. This may be called a network formation."(1)

It is generally assumed that the speed of the flight depends largely on the species involved. All speeds apparently are represented, from that described as "Headlong and precipitous", to that described as "leisurely and slow moving". Most authors agree that the normal flight of the average species is very much modified in migration. Though the local flight may be but a circuitous darting hither and thither, in migration, this becomes direct and purposeful. The records of the actual speed of the flights vary from one-half mile an hour, which is the extreme low limit and is rarely mentioned, up to thirty to sixty miles per hour, though the latter speed is very infrequent. Probably the average speed ranges from six to fifteen miles an hour. Just how much the direction and velocity of the wind have to do with the rate of the flight, has not yet been determined.

A vast amount of information has been gathered descriptive

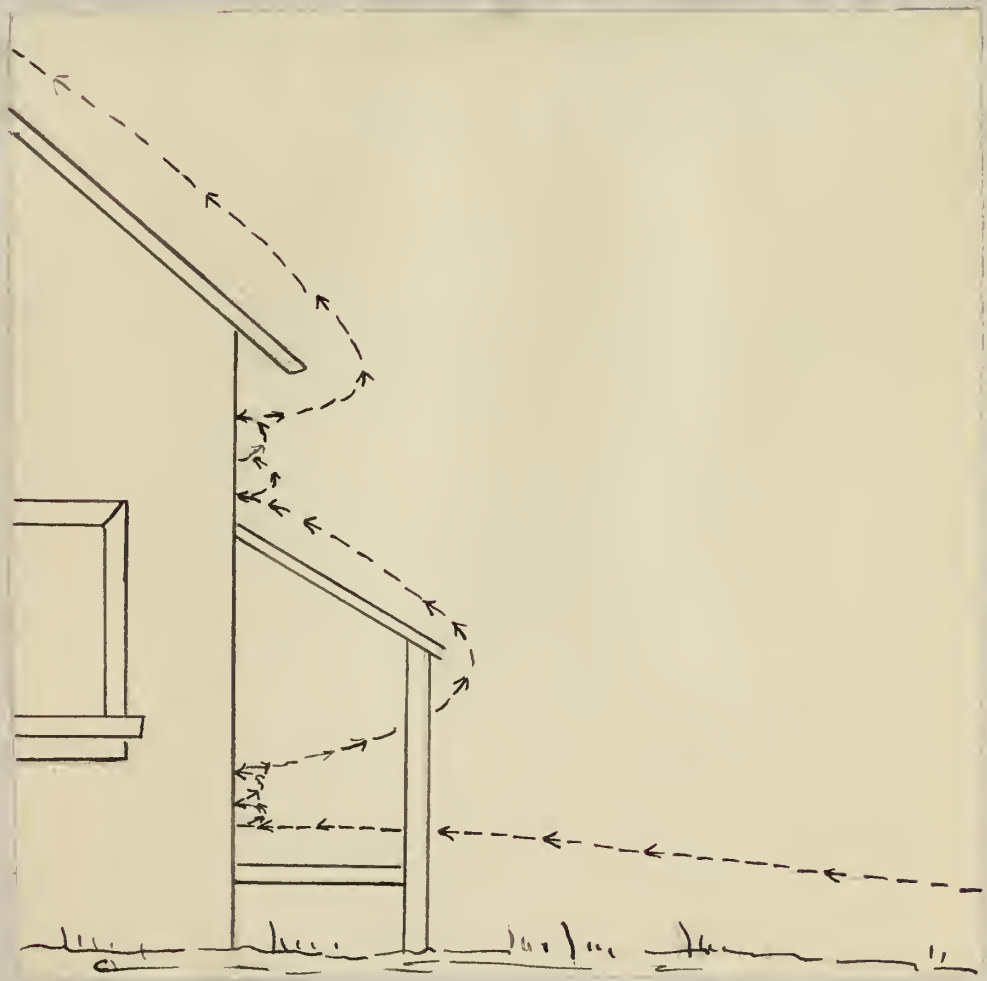
(1) Williams, C.B., Migration of Butterflies. London, Oliver and Boyd. (1930) Page 321.

of the migrants during various stages of the flight. Here too, are found sharply contradictory statements. The consensus seems to be that at the beginning of a flight the insects are in a strong and fresh condition, but that at the end of the flight their conditions vary considerably. Some observers report that all individuals are in good condition, while other observers declare that all individuals are tattered, worn and in a very fatigued condition. Still others assert that some appear in excellent condition with no signs of weariness, while the rest seem tattered and in the last stages of fatigue.

Various species of insects fly at different distances from the ground. Some fly very high, others very low. Insects of fifty different species have been found in the snow on the tops of high mountains. One observer found insects at such high altitudes and believes that they had become numb from the cold. When warmed, however, they revived and flew away. The previously made suggestion that when insect drift in the upper air currents can be studied, it may be found that much migration takes place there, may be fittingly repeated here. Migration may also take place only a little above the level of normal vision. At the moment, however, practically all reliable data deal only with the migrations that take place within a few feet of the ground. Most flight records suggest that the average migration is at the usual height at which butterflies fly - under twenty feet. A notable exception, however, is that of Danais plexippus which will be considered later.

PLATE I

PATH TAKEN BY MIGRATING BUTTERFLY TO PASS AN OBSTACLE



Certain flight features seem to hold true for almost every species. Most important of these is that butterflies never pass broad obstacles, by turning right or left, but always go over them. If, in its flight, a butterfly reaches a house, it rises till it can fly over, then immediately resumes the flight at the original level. In straight ahead flight, the butterfly maintains a practically uniform elevation, dropping where there are declevities in the ground, and rising again where there is a rise in the ground level. Thus the line of flight becomes practically parallel with the earth level.

Godfrey (1927) in writing of butterfly migration in Siam says that a swarm of migrating butterflies had a choice of three paths. One led left and would have taken them to the open sea; the second straight ahead to a village; the third turned right and led eventually to forest outskirts, rich in the type of food which that particular butterfly liked. Almost all took the right hand path, and those that did not, went a short distance and then turned back and took the right path, toward food. Whether the olfactory sense of insects is strong enough to somewhat determine their course is not fully known.(1)

In almost every flight record, a statement of wind direction is given. These vary from flights directly with the wind, to flights directly against the wind. In reading more than two hundred records of various flights, it was noticeable that more

(1) Godfrey, E.J., Migrations of Butterflies in Siam, with some remarks on migrations in general. Journ. of the Siam Soc. Nat. Hist., Bangkok Suppl. 1927. Page 95.

frequent attention was called to flights directly against the wind. Possibly this was due to the fact that the authors tried to explain flights directly against the wind, because these seemed more improbable than flights with the wind. Few records have been made, except by Williams (1930), of flights diagonally with or against the wind. Here again the evidence is so divergent that it is impossible to draw reliable conclusions. Where the flight moves with the wind the natural conclusion is to regard it as involuntary and the insects as carried passively. When the flight is directly against the wind many authors conclude that the sense of smell is so keen in the insects that the pollen odor causes migration. This however seems illogical when in many instances the flight is continued far past a food supply and into regions where food is not abundant. When the flight is diagonally with or against the wind, no attempt is made at an explanation.

What determines the goal in any migration is also largely a matter of conjecture. Some assert that the insect begins flight in an immature condition and that when it becomes sexually mature the migration instinct is suppressed, and it stops in order to deposit its eggs. On the other hand in some cases, migration does not begin until the insect is mature, hence it has to pause early in its flight to deposit its eggs. A second explanation is that insects migrate to find their food plant, and reaching a place where food is abundant the flight ceases. This is not invariably ture, however, because frequently in-

sects will pass regions of abundant food and continue to areas where food is scarce or perhaps not present at all. Another possible explanation is that with the locusts, there are certain physiological changes that arise to suppress the migrating instinct.

In this section it has been possible to discuss but a few of the factors influencing the flight of insects, and a few of the characteristics of the migrants, and of their migration. It would require a much more extended discussion than this presumes to be to adequately examine and weigh all the evidence concerning all of these factors. However, an effort has been made to present a few of the more salient facts, and from these facts to draw some rather definite conclusions.

PLATE II

THE MONARCH

CHAPTER VII

THE MIGRATION OF THE MONARCH BUTTERFLY

Turning from the consideration of general information concerning insect migration, it now may be pertinent to consider specific species of migratory butterflies. Records of butterfly and other insect migration pour in from every continent and from oceanic islands. In many cases, however, too few records of the migrations of one particular species are available, to permit the reaching of any definite conclusions concerning the migration of that species. In many cases there is no certainty as to whether some unusual external circumstance or internal physiological change has caused an individual and specific migration. Following is a list of butterfly families that are definitely known to have the migratory instinct:

1. Papilionidae
2. Pieridae
3. Nymphalidae
    a. Danainae (These very
    b. Nymphalinae (definitely so.
4. Lycaenidae
5. Hesperidae

So little is known about moths that all information is regarded as more or less hypothetical. Therefore, with the exception of a casual mention of specific moths, whose migrations are definitely known to be connected with those of butterflies,

the migrations of moths will not be discussed. In America, the migration of the Monarch Butterfly is best known and most accurately recorded; and in Europe and the British Isles the migration of the Painted Lady provides the greatest wealth of recorded information. It may prove of value to present a detailed description of these two species.

The writer turns first to the migration of the Monarch Butterfly, Danaida plexippus L. This species belongs to subfamily Danainae, of the family Nymphalidae. Synonyms of this species are Danais plexippus, Danais archippus and Anosia plexippus. Accounts of the annual migration of the Monarch come from all over the United States and Canada; from Ontario and Quebec south to Florida and Texas, and from Massachusetts, Connecticut and New York west to Kansas, Missouri, Manitoba and California. Because it has a longer life span than any other species, it is much easier to satisfactorily study its migration. Edwards (1881) and other scientists present evidence to prove that it may live a year or even longer. With twelve months in which to study one group of individuals naturally the evidence is easier to secure and more reliable.(1)

From the entire northern United States and Canada come accounts of Danaida congregating in swarms in the fall. From the farthest northern points swarming seems to occur in September, while farther south the swarms are formed in October. Whether

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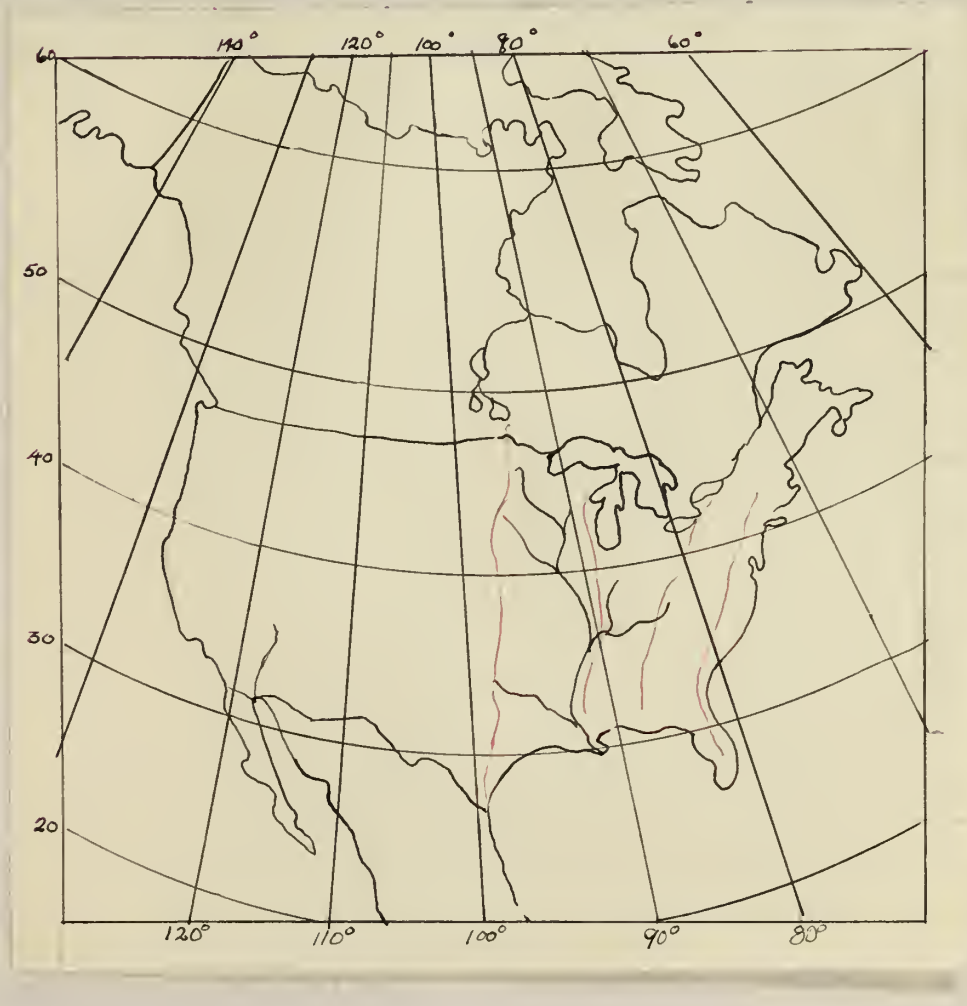
(1) Edwards, W.H., On the Length of Life of Butterflies. Canadian Entomologist, 1881. Vol. 13, Page 214.

PLATE III

MIGRATION ROUTES OF THE MONARCH

(FROM SHANNON)



the butterflies from the more southerly points form separate swarms and proceed southward independently, or whether they join the swarms formed farther north and proceed with them is not accurately known. However, it is indubitably certain that after September and October, except in rare cases, none of this species is ever found in the northern part of the United States and Canada, and huge migrating swarms are seen traveling steadily southward in the southern part of the United States.

Shannon (1915) goes so far as to declare that definite migratory routes can be worked out for the Monarch and asserts that there are four of these separate and distinct flight routes. The first route according to Shannon follows the eastern coast more or less definitely. The second, runs along the shore of Lake Ontario and Lake Erie, and thence southwards, passing west of the Alleghany mountains. He is somewhat indefinite as to its further course. The third, is found to be along the western coast of Lake Michigan and from thence to the lower Mississippi valley. The fourth and the most westerly route goes south from the region of Minneapolis in Minnesota, through Kansas and Oklahoma to Texas. Whether these flight routes are accurate or not must yet be determined. It is certain, however, that much reliable data which comes from points along these routes appears to support his contentions.(1)

The migration of the Monarch continues southward till

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(1) Shannon, H.J., Do Insects migrate like Birds. Harpers Magazine N.Y. 1915. Vol. 131 No. 784, Page 616.

swarms reach Texas, Florida and other southern points where they apparently spend the winter. Records of their winter habits appear to indicate that they spend that season in semi-hibernation. Bromley (1928) writes that everywhere in the Everglades of Florida they can be seen flying and mating. He admits that they may have had their origin in the local Everglades population, but that they appeared to be more like migrants in their winter quarters.(1)

Shepardson, in 1914, published a booklet in which he gave a semi-popular description of the hibernation of the Monarch in California. According to his description they invariably arrive about the second week in October, and remain until March. They gather in swarms in the branches of a special type of Pine tree, found in that particular locality. While oaks are present in abundance, yet for some reason they never settle upon these trees. In fine weather they group themselves on the tips of the branches of the pine trees and during rain or cold move inward to the trunks where they cluster with the bright side of their wings folded inward and the dull side out. On warm and sunny days, the individuals go forth in search of nectar, which is their food; but in rainy weather they rarely or never move. No matter how far afield they go during the day, they always return to the same tree at night. The birds in the locality appear not to bother them at all, although a

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(1) Bromley, S.W., The Monarch Butterfly wintering in the Everglades. Entomological News (1928). Vol. 39,Pages 96-97.

particularly greedy type of jay is common in that area. About the first of March the Monarch gradually disappears and during the summer is as completely absent from that region as from the north in the winter.(1)

The so-called northward migration of this species can with accuracy scarcely be termed a migration, since the insects never travel northward in swarms. Rather, they travel entirely separately, stopping along the way to deposit their eggs.Thus the complete northward journey may not be made by any one individual, but rather by representatives of successive broods. Just how many different broods there may be in one particular locality has not been ascertained with certainty, but probably in some regions there may be two, in others three, while some even report four. Much fuller information must be obtained concerning the northward migration of the Monarch; whether one individual ever makes the complete journey, how many broods there are according to geographic localities etc., before satisfactory conclusions can be arrived at. Scattered individuals of the species have been found as far north as Hudson Bay, although it is not generally believed that breeding takes place there. The records of successive broods from various places help to date the speed of the northern migration.

Probably the details of the migration of Danaida plexippus are better known than those of any other species in the

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(1) Shepardson, L., The Butterfly Trees. San Francisco, 1914. Pages 1-32.

world. The time element is definitely established, also the geographic distribution. Much has been recorded about their spread to Europe and the Pacific. Earlier in this paper the writer commented on reports that Danaida had been carried in potato lockers to England. The fact, however, that in only one instance has the insect been seen in the British Isles in the spring, though seen many times in the fall, leads to another possible explanation. Since they are invariably seen in the autumn it seems possible that instead of following the normal migratory route southward in the United States they, for some unknown reason, have turned or been turned aside from their regular path and the migration, whether voluntary or involuntary, has been directly across the Atlantic to England. This point of view is substantiated by the fact that various observers on ocean liners report having seen scattered individuals far from land, but apparently migrating toward the British Isles. But the facts relative to their migration in the United States present those migrations as so regular and uniform, that some authors compare the southward migration of the Monarch to the annual fall flight of the migratory species of birds.

PLATE IV

THE PAINTED LADY

CHAPTER VIII

THE MIGRATION OF THE PAINTED LADY

Equally interesting are the migrations of the Painted Lady, Vanessa cardui L. (synonyms Pyrameis cardui and Cynthia cardui). Its migratory flight shows two distinct differences from that of the Monarch. Apparently the magnitude and scope of the migration of Danais plexippus is relatively the same each successive year, while Vanessa cardui is so much more common in some years than in others, that certain years have been called "Painted Lady years", due to the uncommon abundance of this particular species. The second difference is that while the Monarch migrates northward individually, it migrates southward in huge swarms. But precisely the opposite is true of Vanessa cardui, whose northern migratory journey is made in swarms, while there is much uncertainty as to whether a return southern migration is ever made. Of course if there is no southern migration there is an enormous loss of life, since there is no definite evidence that the insects hibernate to any extent in the northern climates. However, there is but one record of a southerly migration, and while there is the possible supposition that it is comparable to the northern migration of the Monarch, much more reliable information is necessary before we can accept this hypothesis. Vanessa cardui is the most cosmopolitan of all our butterflies. It is found on everyone of the continents, rang-

ing from the equator to within a short distance of the arctic circle. While in some years scarcely a single individual is noted in continental Europe and the British Isles, in other years both it and its migrating companion, Plusia gamma are very abundant; and in a few isolated years, called "Painted Lady years", the migrating hordes of this species are stupendous. Such years were 1879, 1903 and 1926, and since the spread of migration varies in each case, it may be well to consider them separately.

The geographic origin of Vanessa cardui is more or less uncertain since in a very few cases, and perhaps really accurately in no case, has anyone actually seen the beginning of a migratory flight. But there exists evidence which suggests that they come from the Southeastern Desert of North Africa and pass northward through the southern Nile Valley. They have also been seen in Mesopotamia, in Palestine, in the Egyptian Desert near the border of the Sudan, and there is a report that they have been observed in Nigeria. Their most northerly spread is Scandanavia, Russia and Iceland.(1)

The records show that between April fifteenth and twentieth of the 1879 migration the insects traveled in a northeasterly direction from North West Africa and Algiers. From the first to third of May they were seen in Valencia and Bar-

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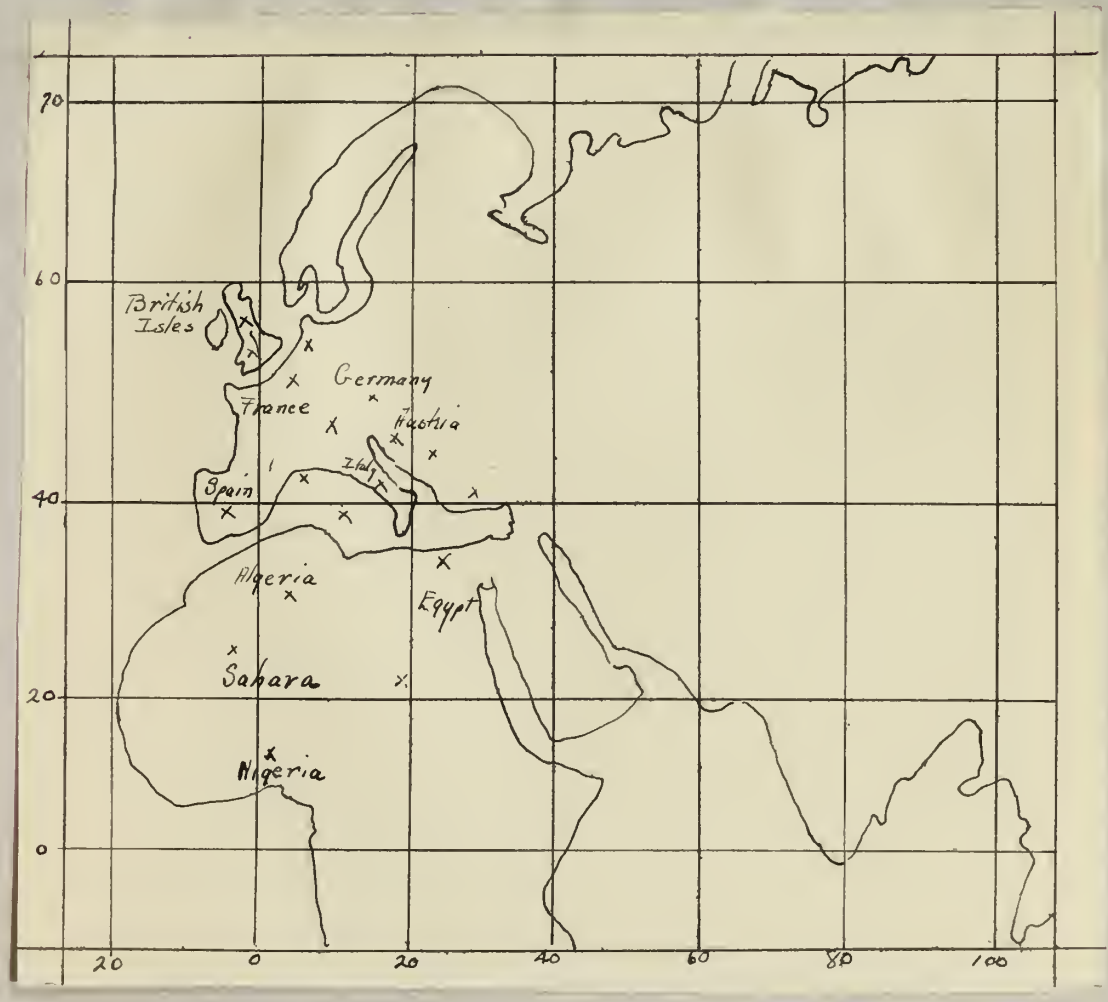
(1) Williams, C.B., Migration of the Painted Lady Butterfly. Nature 1925. Vol. 115, Page 535.

PLATE V

LOCALITIES WHERE MIGRATIONS OF THE PAINTED LADY HAVE BEEN RECORDED



celona, as well as in Minorca. At the end of May they had spread into France, while on June first they were seen in Switzerland at the Hospice of Saint Gothard, and in England between June ten and thirteen.(1) It will be noticed that there was very little activity during the month of May, and during July the insects were again inactive. Reports indicate that again in late August other migrations occurred, particularly in France and England. Probably this case is again comparable to the Monarch; the August migration being made undoubtedly by a later brood than that of the April migration.

Various opinions are expressed by authors of that period as to the cause of the uncommon abundance. One writer states that it was not due to migration from Africa, as some French and Swiss journals suggest, but was due to a local fecundity of the butterfly.(2) Another writer hotly contradicts this statement, declaring that the insects must have migrated; that the countless numbers could not have been due to local fecundity.(3) The consensus seems to be that, in general, the year was particularly poor for insects, having been both cold and wet.

The 1903 migration seems to have been very different, since no records of the flight come from Africa, and South Europe. Suddenly in July the insects appeared in vast numbers in cen-

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(1) Tutt, J.W., Migration and Dispersal of Insects: Lepidoptera Entomologist's Record 1900. Vol. 12, Page 155.
(2) Forel, F.A., Butterfly Swarms. Nature 1879. Vol. 20, Page 197.
(3) Haines, F.H.,Butterfly Swarms. Nature 1879 Vol. 20, Page 243.

tral Europe. No further mention is made of them until late September and early October, when reports of the invasion of France and the British Isles by the Painted Lady were made by many observers.

By the time the 1926 migration took place, people were giving the matter of insect migration such attention that the data gathered are much more accurate and detailed, than those of the migrations of 1879 and 1903. This evidence points to two general migrations. Williams (1930) writes that during April and May "large swarms were seen moving more or less northward in Egypt, Palestine, Transjordania and the Caucasus, and some were even seen crossing the Mediterranean." Then about the third week in July, the insects were found in abundance in Italy, Germany and England.(1)

Since the evidence supports the theory that the source of the migrations is in the South Desert of North Africe, it is particularly interesting to quote Skertchly(1879). "Some at least of the swarms of V. cardui originate in Africa, one of which I witnessed a day's march west of Sowakin, in Nubia in March 1869. Our caravan had started for the coast, leaving the mountains shrouded in heavy clouds, soon after daybreak. At the foot of the high country is a stretch of wiry grass, beyond which lies the rainless desert as far as the sea. From my camel I noticed that the whole mass of the grass seemed violently agitated, although

(1) Williams, C.B., Migration of Butterflies. London, Oliver and Boyd. 1930. Page 209.

there was no wind. On dismounting I found that the motion was caused by the contortions of pupae of V. cardui, which were so numerous that almost every blade of grass seemed to bear one. The effect of these wrigglings was most peculiar - as if each grass stem was shaken separately, as indeed was the case, instead of bending before the breeze. I called the attention of the late J. K. Lord to the phenomenon, and we awaited the result. Presently the pupae began to burst and the red fluid that escaped, sprinkled the ground like a rain of blood. Myriads of butterflies, limp and helpless, sprinkled the ground. Presently the sun shone forth and the insects began to dry their wings, and about half an hour after the birth of the first, the whole swarm rose as a dense cloud and flew eastwards toward the sea. I do not know how long the swarm was, but it was certainly more than a mile, and its breadth exceeded a quarter of a mile."(1)

Williams suggests that the swarms which migrate into California each spring seem to come from Mexico northward. And he adds that apparently the first act of any migrating swarm of Vanessa cardui is to cross a large stretch of desert.(2)

The dates of the stages of the northward migration depend seemingly upon the particular migration. The sex organs are apparently undeveloped at the time of the beginning of the

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(1) Skertchly, S.B.J., Butterfly Swarms. Nature 1879. Vol. 20, Page 266.
(2) Williams, C.B., The Migration of Butterflies. London, Oliver Boyd and Co., 1930. Page 209.

flight. As the insects attain sexual maturity they pause and lay their eggs on the thistles, which are found in all localities. Whether that first generation finishes the journey is a matter of conjecture. At any rate while the northward migration begins in March or April, immigrants usually arrive in England about the middle of May, the records of their arrival being too numerous to mention. The general westward flight passes Heligoland in the North sea, and many reports come from there concerning the clouds of Vanessa cardui accompanied by Plusia gamma.

Reports of scattered adults of Vanessa cardui found flying in England every month in the year are quite numerous, but information concerning their possible hibernation in that country is too unreliable to form a basis for scientific conclusions. The possibility of a southward journey has already been discussed.

CHAPTER IX

CONCLUSION

From the foregoing it is clearly evident that the subject of insect migration is still in its earliest stages of development. Throughout the entire study the need of further evidence and more reliable date from which to draw conclusions has been apparent. Where do the great migrating bands originate, what really motivates the movement, is there a return migration in the case of Vanessa cardui, where do the swarms of Vanessa cardui originate? These and many other problems confront the earnest investigator.

It is clear that these questions can never be answered by mere speculation. More and more the need of further evidence has been impressed upon the writer. Since the appeal of Mr. Williams for better scientific cooperation to secure reliable data, it has been evident that many new observers are taking part in the search for facts, and that his plea for more careful accuracy in the making of records of observations is proving effective. Every serious student of this subject is fully aware of the great debt which the scientific world owes that author for the vast wealth of evidence which he has collected and for his painstaking and patient sifting of a stupendous amount of material, in order to separate fact from fancy.

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GRADUATE SCHOOL

A Digest of the Thesis

THE MIGRATION OF INSECTS

(With Special Reference To Butterflies)

by

Leota Carolene Colpitts

(A.B., Wellesley College, 1924)

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A DIGEST OF THE THESIS

THE MIGRATION OF INSECTS (WITH SPECIAL REFERENCE TO THE BUTTERFLIES)

From earliest historical times, come references to the migration of insects. Beginning about 1850, the references become more numerous, and every year new evidence accumulates coming from every corner of the globe. The great migration of the Painted Lady in 1879, seems to have acted as a stimulus to investigators.

Two factors have contributed toward making the study of the migration of insects a difficult one. First, until recently the larger part of the records were unscientific in nature. Second, the migrations differ so greatly with various species of insects, and even in different flights of the same insect, that a sufficient amount of data, from which to draw conclusions are lacking.

In comparing the migration of birds and fish with that of insects, it is evident that the migrations of the former are purposeful and regularly recurrent, and that they always make a return migration. Migration in the lemming is much more like that of insects, in that it is not regular in recurrence, there is no return migration and all individuals do not participate in a given movement.

Investigators differ greatly as to what constitutes a

satisfactory definition for migration as applied to insects. The definition chosen as a basis for the discussion in this paper is that of Williams which he gives in the following terms: "Migration is a periodic, more or less unidirectional, continued movement, assisted by the efforts of the animal in a direction over which it exerts a control which results in the animal passing away from its previous daily field of operation."

Prior to a statement of the suspected causes of migration, it may be suggested that the circumstances which led scientists to believe certain groups of insects showed migratory characteristics were: first, flights seen in progress; second, butterflies not endemic to a certain region suddenly appearing there; third, the disappearance of insects from regions where they were endemic; and fourth, insects reported in places which could never be their normal habitat.

Some authors regard insect migration as a purely passive act, and due entirely to outside forces, the agents being air currents and ships. While migration in certain instances may be passive, nevertheless this cannot satisfactorily account for all migrations of insects. What then is the cause for the migratory instinct suddenly becoming active? The chief causes assigned are lack of the larval food supply, and over-population; but rythym, sex impulse, and parisitism have also been suggested as causes.

The explanation by Uvarov of the migration of Locusts proved too interesting to omit. His theory is that there are

three forms of the one species, Locusta migratoria L. The ability to migrate depends on the ability of the swarming form migratorioides to transform itself into the solitary form danica, with migratoria as the half way phase. Uvarov says: "The periodicity of the locust invasions is caused entirely by the wonderful phenomenon of the transformation of the swarming locust into a solitary harmless grasshopper."

Much exceedingly interesting information has been gathered concerning the migrants and the various recorded migratory flights. The consensus seems to be that migrants are usually fresh at the start of a flight, and that they are worn, tattered and tired at the end of it. Most evidence seems to point to the fact that migration usually starts when the insect is in a sexually immature state. The speed of flights seems to vary considerably, some being as slow as one-half mile per hour ranging from this low point to a high point of 30-60 miles an hour, with an average speed of 6-15 miles per hour. The flight is usually maintained at a uniform height from the ground, the tendency being always to rise to avoid an obstacle. Much has been said concerning wind direction in relation to flight. More records give flight with, or against, the wind, possibly because they are most easy to record. Williams seems to be the only one to contribute much material concerning flights diagonally with or against the wind.

The migration of Danaida plexippus in the United States offers a very interesting study. Every year huge swarms of mi-

grating Monarchs are seen making their way southward from as far north as Manitoba, and from the Atlantic Ocean to Kansas. The migrations are regularly recurrent every fall, and evidence seems to indicate that the insects spend the winter in the southern United States and then fly north in the spring not in migrating swarms, but individually. There is no evidence that the same individual makes the entire northern journey. Perhaps it is made by representatives from successive broods, although the length of life of Danaida plexippus may be at best, one year. No such accurate records are to be had of the migration of any other species.

In continental Europe and the British Isles, the Painted Lady is the most common migrant, although the migrations do not recurr regularly. Some years few or no migrating Vanessa cardui will be seen, while other years there will be such an abundance, that they will be known as "Painted Lady" years. The primary breeding place of Vanessa cardui has never been accurately determined but records come from Egypt, the African deserts, and even Nigeria. Vanessa cardui migrates northward in the spring and early summer in huge bands and contrary to the Monarch there is no evidence of a southward migration. The three years having largest migrations of this species were 1879, 1903 and 1926, with records showing that it occurred as far north as Iceland.

Much vital information is still lacking concerning the migration of insects, but each year more information is being

gathered, and in time it will be possible to draw much more accurate conclusions, than can now be reached with the present limited data.

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